PHOTOBIOLOGY OF THE SYMBIOTIC SEA ANEMONE *ANTHOPLEURA ELEGANTISSIMA:* PHOTOSYNTHESIS, RESPIRATION, AND BEHAVIOR UNDER INTERTIDAL CONDITIONS

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ABSTRACT

Continually immersed specimens of *Anthopleura elegantissima* freshly collected from the shore receive at least 34–42% of their respiratory carbon requirement from their endosymbiotic zooxanthellae. This value decreases to 17% when intertidal sea anemones are exposed to air for 15 h during daytime spring low tides, primarily owing to a reduction in photosynthesis by the algae, which are shaded when the anemone retracts its tentacles and contracts its marginal sphincter. Contraction of continually immersed anemones during peak irradiance likewise decreases their photosynthesis. This behavior is primarily in response to high levels of intracellular oxygen generated by the symbiotic algae, although ultraviolet radiation also causes contraction, especially in aposymbiotic individuals which have lower concentrations of UV-B absorbing substances than do symbiotic anemones. Although *A. elegantissima* may vary its photosynthetic capacity according to long-term average light conditions, behavioral adaptations such as contraction and attachment of debris to the column verrucae protect the animal and its algal symbionts from deleterious photodynamic effects during short-term exposure to peak levels of irradiance.

INTRODUCTION

Anthopleura elegantissima (Brandt) is the most abundant sea anemone on the west coast of North America (Hand, 1955) and has a vertical range from 0 (mean lower low water) to more than +2 m above tidal datum (Hand, 1955; Littler *et al.,* 1983). At the latter tidal height the anemone is exposed to air approximately 90% of the time (Ricketts, 1934), frequently for several days without immersion (Fig. 1). The morphological (Francis, 1973; Shick *et al.,* 1979), reproductive (Francis, 1973; Sebens, 1980, 1981; 1982a, b), behavioral (Hart and Crowe, 1977; Shick, 1981), and physiological (Hart and Crowe, 1977; Shick, 1981) adaptations contributing to success under such physically stressful conditions have received much attention, as have the community ecological ramifications of the dominance of large areas of substrate by this anemone (Taylor and Littler, 1982).

Although it has not been stated explicitly, the nutritional contribution by this sea anemone's endosymbiotic dinoflagellates (zooxanthellae) must also be a major factor allowing a sessile suspension feeder to exist in the food-limited upper intertidal zone, and *A. elegantissima* indeed ranks among the top primary producers in its habitat, based on measurements of photosynthesis and respiration in submerged individuals

(Fitt *et al.,* 1982). The ability of intertidal macroalgae to maintain photosynthesis during aerial exposure is directly correlated with their height of occurrence on the shore (Johnson *et al.,* 1974; Brinkhuis *et al.,* 1976; Quadir *et al.,* 1979; Beer and Eshel, 1983), but there have been no such studies on sea anemones. In the present paper we examine the effects of emersion on both photosynthesis and respiration in *A. elegantissima* under natural conditions of exposure and illumination.

Occupation of the intertidal zone also exposes soft bodied organisms directly to a high photon flux which has demonstrable deleterious effects on coral reef invertebrates (Jokiel, 1980; Jokiel and York, 1982; Olson, 1983). Because symbiotic individuals of *A. elegantissima* have behavioral (Pearse, 1974) and biochemical (Buchsbaum, 1968) adaptations to protect themselves against high levels of irradiance, we have extended our study to examine these defensive mechanisms and their implications for the productivity of this symbiosis.

MATERIALS AND METHODS

Collection of specimens

Most specimens of *Anthopleura elegantissima* were collected on the south jetty at Bodega Harbor, California, from several clones at mean lower low water, and from a second group of clones 1.3 m above the first. These intertidal heights are the same as in our earlier study of this species (Shick, 1981); the exposure regime experienced by these anemones at the time of the various experiments (June 1980, 1982, and 1983) can be seen in the tidal curve in Figure 1. This season was chosen to minimize the difference between air and sea water temperatures while maximizing periods of intertidal exposure during daylight hours at the site.

Measurement of photosynthesis and respiration

All anemones were cleaned of adhering debris and used within 60 h (usually within 24 h) of collection. They were not fed during maintenance in the flowing sea
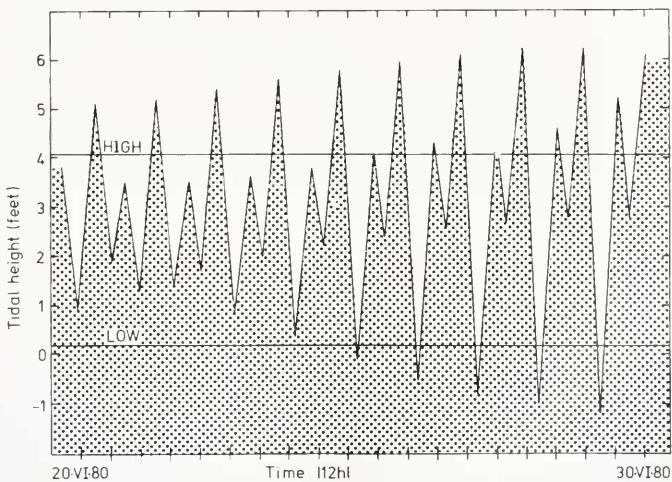

FIGURE 1.   Tidal curve at Bodega Harbor, California, for 20–30 June 1980. "High" and "low" indicate intertidal heights on the south jetty at which the anemones in this study were collected.

water system at the Bodega Marine Laboratory, University of California, prior to the experiments. Photosynthesis and respiration were measured as oxygen fluxes at 15°C in air and in Millipore filtered (0.45 μm pore size) sea water in Gilson all-glass submarine respirometers, the contents of which were continuously stirred with magnetic spinbars, with at least hourly venting to the atmosphere. Aerial and aquatic measurements of oxygen fluxes under natural light conditions were synchronized to coincide with emersion and immersion of anemones at the two intertidal heights on the jetty. The temperature-stabilized respirometers, located in the courtyard of the Bodega Marine Laboratory, were situated to simulate the light and shade patterns experienced by the anemones on the jetty. All experiments were conducted on days which had fog in the morning and light overcast in the afternoon.

Chlorophyll and protein determinations

Zooxanthella:animal biomass ratios (symbolized as $1-\beta$, following Muscatine *et al.*, 1981) of the individual sea anemones were determined by the method of McKinney (1978), with modifications. Briefly, individual anemones were weighed and then homogenized in 10 cm^3 Moore's calcium-free artificial sea water (Cavanaugh, 1975) with 0.5 mM EDTA added, in a Brinkmann Polytron homogenizer. Total protein (zooxanthellae plus animal tissue) was measured on one aliquot of the crude homogenate using the Coomassie brilliant blue technique (Bradford, 1976) after digestion in 5% NaOH. Following two 10-h extractions in 90% acetone, total chlorophyll (*a* and c_2) was measured according to the method of Jeffrey and Humphrey (1975). Intact zooxanthellae were separated from animal tissue in another aliquot of the homogenate by centrifugation at $900 \times g$ in a three-step 84–21% sucrose density gradient in a Sorvall HB-4 swinging bucket rotor. The zooxanthella fraction, which accumulated at the 84–63% sucrose interface, was washed at least five times in calcium-free sea water and checked for integrity and purity under a Zeiss fluorescence microscope. The protein and chlorophyll contents of cleaned zooxanthellae were determined as for whole anemones. The zooxanthella protein:chlorophyll ratio was multiplied by the total chlorophyll content of the intact anemone, and the product was subtracted from total anemone protein, to give the animal protein content. The oxygen uptake (N_{O_2}) by living anemones could then be partitioned into zooxanthella and animal N_{O_2}, as discussed in Muscatine *et al.* (1981).

The presence of UV-B (wavelengths between 280 and 320 nm) absorbing substances in symbiotic and aposymbiotic (lacking zooxanthellae) anemones was checked according to the method of Jokiel and York (1982). Aliquots of the homogenates from the chlorophyll determinations were extracted in a 1:6 dilution with distilled water, placed in quartz cuvettes, and scanned on a calibrated Shimadzu spectrophotometer. The peak with an absorbance maximum at 320 nm was quantified in both groups of anemones.

Direct calorimetry

To confirm that intertidal specimens of *A. elegantissima* remain fully aerobic during emersion, coordinated measurements of oxygen uptake ($\dot{n}_{O_2}$, μg $O_2 \cdot h^{-1} \cdot g^{-1}$) and heat dissipation ($_t\dot{q}$, mW $\cdot$ g^{-1}) were made. Freshly collected anemones were transported to our laboratory in Maine, maintained for 4 days without feeding at their normal exposure regime in a tidal simulator, and their $\dot{n}_{O_2}$ and $_t\dot{q}$ measured in the dark during their normal exposure period, as described in Shick (1981). Rates of oxygen consumption were compared to rates of heat dissipation using a standard oxycaloric equivalent of 1 mg $O_2 \cdot h^{-1}$ = 3.906 mW (Gnaiger, 1983).

Contribution of zooxanthella carbon to animal respiration

Oxygen flux data [μg $O_2 \cdot$ (mg anemone dry weight)$^{-1} \cdot h^{-1}$] were converted to carbon equivalents, assuming a zooxanthella photosynthetic quotient (PQ) of 1.0 (Muscatine *et al.*, 1981) and an anemone respiratory quotient (RQ) of 1.0 (Fitt and Pardy, 1981), to enable the calculation of the contribution of translocated zooxanthella carbon to the host animal's respiratory demand (CZAR) using the equation of Muscatine *et al.* (1981). This calculation was further based on measured zooxanthella:animal protein biomass ratios of 0.026 ± 0.008 (S.D.) and 0.034 ± 0.016 in high and low shore anemones, respectively, and a zooxanthella photosynthate translocation factor of 40% (Trench, 1971). For additional assumptions of the method, see Muscatine *et al.* (1981).

Behavioral responses to illumination

Groups of 15 mid-intertidal anemones were exposed to seven experimental conditions of illumination during continuous immersion. The degree of expansion or contraction of individual anemones was noted hourly during daylight and occasionally at night for 2.5 days. Expansion state was scored as: 0—tentacles fully retracted and marginal sphincter contracted; 1—25% of oral disk exposed; 2—50% of oral disk exposed; 3—75% of oral disk exposed; 4—oral disk completely exposed and tentacles fully extended. Experimental conditions during the behavioral observations were as follows: 1) symbiotic anemones in full sunlight during daylight hours (normal); 2) symbiotic anemones in full sunlight but beneath a clear glass plate to block ultraviolet radiation (UV-blocked); 3) symbiotic anemones exposed to 1×10^{-5} M DCMU, an inhibitor of photosynthesis (DCMU); 4) aposymbiotic anemones (lacking zooxanthellae) in full sunlight (Apo); 5) Apo-UV blocked; 6) symbiotic anemones in the laboratory under dim artificial light (maximum irradiance 25 μEinsteins $\cdot m^{-2} \cdot s^{-1}$) (Dim); and 7) Apo-Dim.

<center>RESULTS</center>

Rates of respiration and photosynthesis by high and low intertidal *A. elegantissima* are shown in Figure 2, as is the range of light intensity measured hourly on the several days of these experiments. Negative values for oxygen flux ($\dot{n}_{O_2}$) indicate net oxygen consumption; positive values show net oxygen production.

The coordinated measurements of $_t\dot{q}$ and $\dot{n}_{O_2}$ indicated that intertidal anemones remained fully aerobic during 15 h in air, so that measurements of oxygen uptake can be used to quantify total energy metabolism. Directly measured $_t\dot{q}$ was 1.139 mW $\cdot$ (g dry weight)$^{-1}$ ± 0.129 (S.D.)., and the caloric equivalent of $\dot{n}_{O_2}$ was 1.198 ± 0.054 mW $\cdot g^{-1}$ during the last 12 h in air. These mean rates are not significantly different ($t = 0.941$, df = 8, $P > .10$).

Zooxanthella:animal biomass ratios (1-β), total chlorophyll concentrations, net photosynthesis by zooxanthellae (P_z net, in carbon equivalents), animal respiration (R_a, in carbon equivalents), and CZAR are presented in Table I. Also shown are the results of *t*-tests between the means of these values in low and high shore anemones, and between means of low shore anemones and high shore anemones measured during continuous immersion. There are no significant differences between low and high shore specimens in 1-β or total chlorophyll concentration. The large reduction in CZAR in high shore relative to low shore anemones is due primarily to the reduction in P_z net in the former. Consistent but insignificant differences in P_z net and R_a between low shore anemones and high shore conspecifics measured during continuous immersion combined to produce a significantly greater CZAR in the latter.
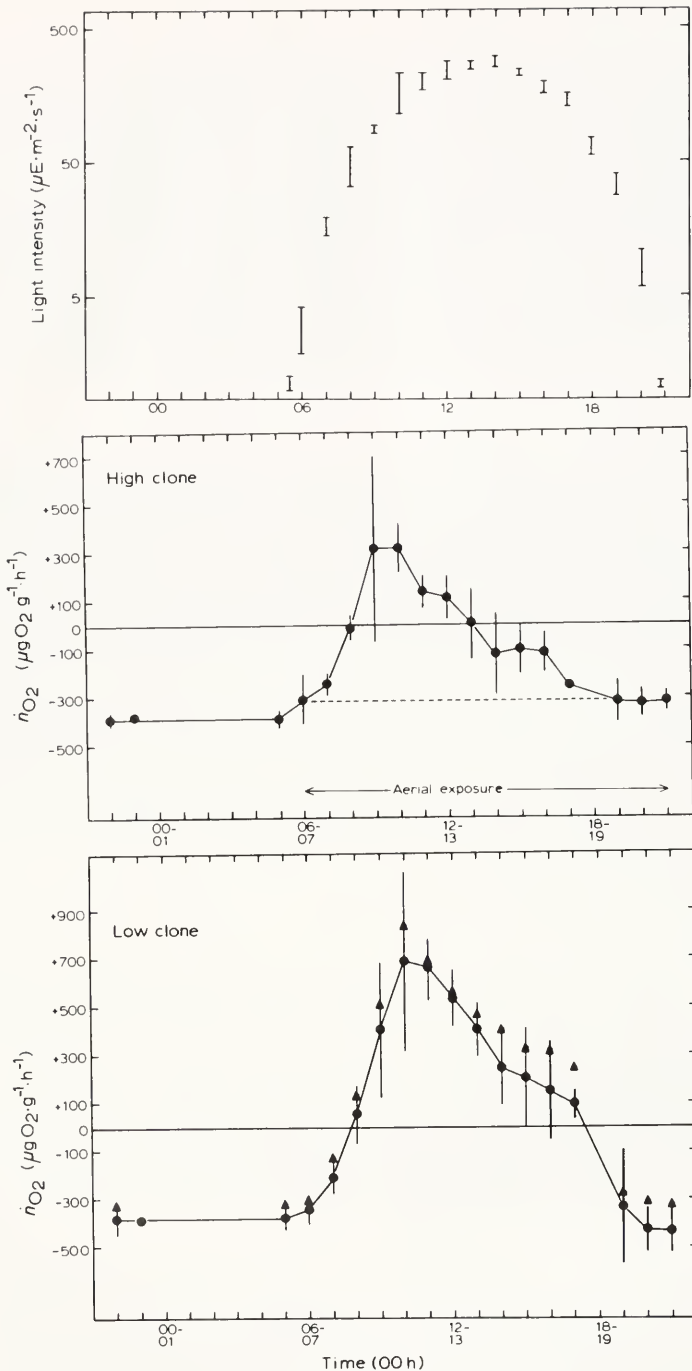
FIGURE 2. Hourly light intensity (irradiance) and oxygen flux ($\dot{n}_{O_2}$) in high and low shore specimens of *Anthopleura elegantissima* measured under natural conditions of ambient sunlight and intertidal exposure. Hours are in Pacific Daylight Time. Vertical bars indicate the range of hourly irradiance during the three days of the measurements; values for $\dot{n}_{O_2}$ are means and 95% confidence intervals. The duration of aerial exposure in the high shore anemones is indicated by the horizontal line. Also shown are the mean values (triangles) for $\dot{n}_{O_2}$ in two high shore specimens measured under low shore (continuous immersion) conditions. Oxygen flux data have not been weight adjusted, as mean weights for high and low shore anemones were the same [high: 0.549 ± 0.132 (S.D.) g dry weight; low: 0.534 ± 0.125 g dry weight)].

TABLE I

Components of organic productivity in high and low shore Anthopleura elegantissima, and in high shore anemones under low shore (continuous immersion) conditions (High/S)

	1-β	Chl	$P_z$net†	R_a†	CZAR†
High	0.026 ± 0.008 (10)	0.331 ± 0.069 (10)	1.255 ± 0.046 (4)	2.853 ± 0.297 (4)	17.7 ± 1.6 (4)
	} NS	} NS	} **	} NS	} **
Low	0.034 ± 0.016 (10)	0.357 ± 0.098 (10)	2.713 ± 0.046 (4)	3.193 ± 0.260 (4)	34.0 ± 1.6 (4)
	} NS	} NS	} NS	} NS	} *
High/S	0.033 ± 0.024 (2)	0.328 ± 0.193 (2)	2.858 ± 0.047 (2)	2.748 ± 0.141 (2)	41.6 ± 1.4 (2)

1-β = zooxanthella:animal biomass ratio; Chl = total chlorophyll concentration ($a + c_2$, μg per mg anemone dry weight); P_z net = net production by zooxanthellae (mg C·day^{-1}); R_a = animal respiration (mg C·day^{-1}); CZAR = contribution of zooxanthellae translocated carbon to the animal's daily respiration (percent). Values are means ± S.D. (N). Results of Student's t-tests are expressed as: NS ($P > .05$); *($P < .01$); **($P < .001$).

† $P_z$net, R_a, and CZAR have been calculated from the data in Figure 2, where high shore anemones have a mean body dry weight of 0.549 ± 0.132 (S.D.) g, and low shore anemones weigh 0.534 ± 0.125 g.
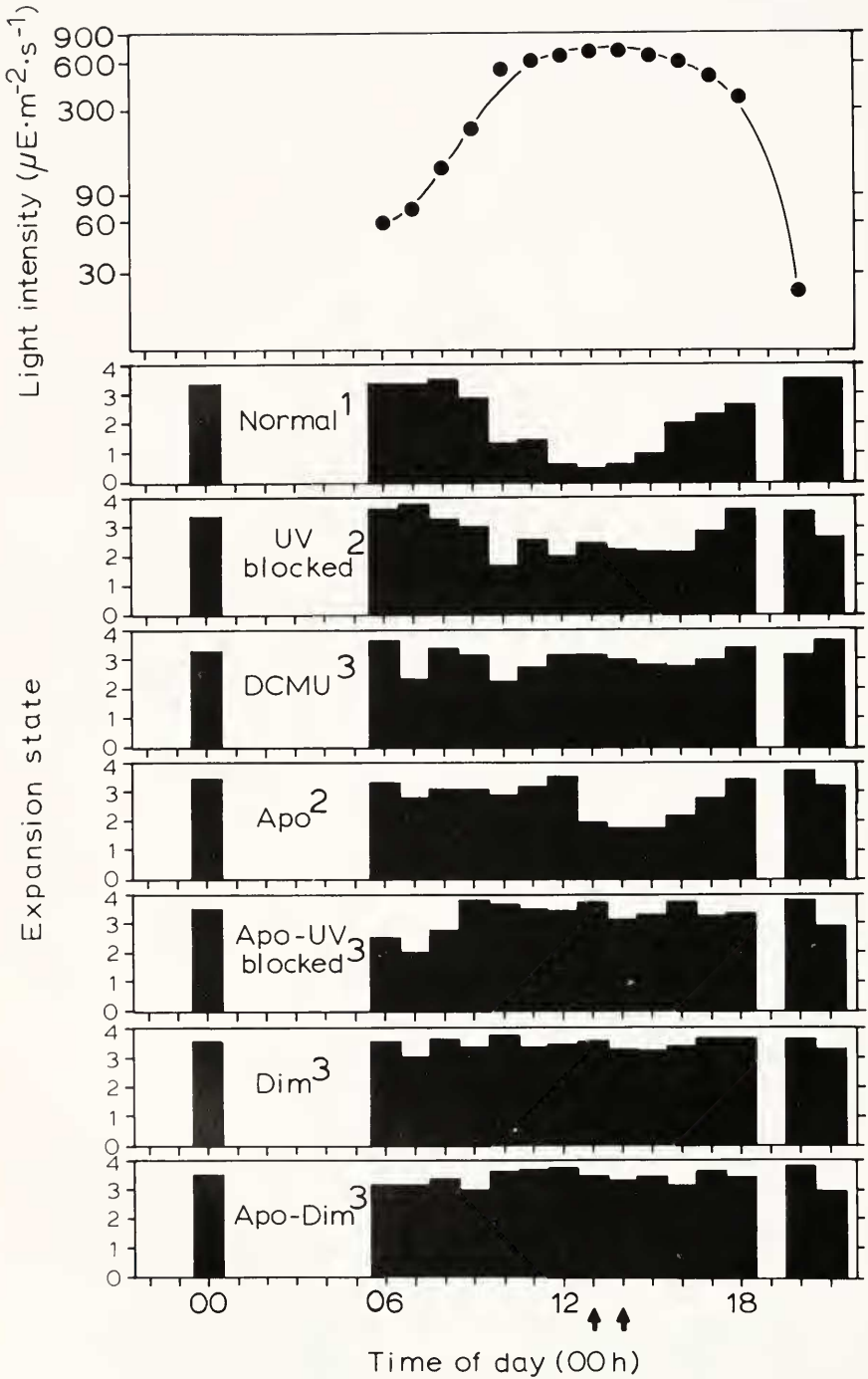
FIGURE 3.   Sunlight intensity (irradiance) and mean expansion state in mid-shore *Anthopleura ele-gantissima* under continuous immersion. Values of light intensity are hourly means on the two days of the experiments. Bars indicate the mean expansion state of 15 anemones in each treatment group measured on two consecutive days. "Dim" and "Apo-dim" anemones were maintained in the laboratory at a maximum

The high absorbance at 320 nm by aqueous extracts of symbiotic specimens of *A. elegantissima* may indicate the presence of the S-320 pigment described by Shibata (1969), and investigated further by Jokiel and York (1982), in a variety of corals. There was no difference between low and high intertidal symbiotic anemones in their UV-B absorbance (*t*-test, $P > .10$), so these data were pooled. Symbiotic anemones had a higher UV-B absorbance [0.581 absorbance units per gram anemone wet weight ± 0.208 (S.D.), n = 20] than did aposymbiotic specimens (0.168 ± 0.113 absorbance units per gram, n = 10; $t = 5.295$, df = 28, $P < .001$).

Results of the behavior experiments are presented in Figure 3, as are the mean light intensities measured at the times of the observations of the anemones during the 2.5 days of the study. The degree of expansion of symbiotic anemones in natural sunlight was inversely related to light intensity above approximately 200–300 μEinsteins $\cdot$ m^{-2} $\cdot$ s^{-1}. When symbiotic anemones were screened from UV radiation the results were qualitatively similar, but analysis of variance and Student-Newman-Keuls multiple comparison test applied to the pooled data for the two hours of maximum irradiance (1300 and 1400 h Pacific Daylight Time) revealed that the extent of contraction was less than in symbiotic anemones not shielded from UV (Fig. 3). Inhibition of zooxanthella photosynthesis by DCMU eliminated the contraction response of symbiotic anemones to natural sunlight, but aposymbiotic anemones nevertheless did contract at midday despite their lack of zooxanthellae. Screening aposymbiotic anemones from UV eliminated this contraction, probably because these anemones had a lower concentration of UV-B absorbing substances than did symbiotic specimens. Freshly collected anemones maintained under dim illumination remained fully expanded throughout the experiment, which suggests that there is no tidal or circadian rhythm of contraction.

DISCUSSION

As in our previous studies of intertidal sea anemones (Shick *et al.*, 1979; Shick, 1981), exposure of *Anthopleura elegantissima* to air resulted in a decrease in the rate of oxygen uptake ($\dot{n}_{O_2}$) in the dark (Fig. 2). The absence of an oxygen debt (enhanced $\dot{n}_{O_2}$) in intertidally acclimatized *A. elegantissima* upon reimmersion was taken to indicate their lack of reliance on anaerobic metabolism during exposure (Shick, 1981). This has now been confirmed using coordinated measurements of heat dissipation ($_t\dot{q}$) and oxygen uptake during 15 h in air: the agreement of measured $_t\dot{q}$ with that predicted from $\dot{n}_{O_2}$ demonstrates that there is no anaerobic contribution to total metabolic heat dissipation during emersion. Although contraction in air presumably causes tissue hypoxia (and hence, diminished $\dot{n}_{O_2}$) by decreasing the surface area:mass ratio and by increasing diffusion distances in tissues (Shick *et al.*, 1979), this is offset to some extent by a continuing irrigation of the coelenteron during exposure. We have observed that intertidally-acclimatized anemones pump water out of the coelenteron, onto the exposed oral disk, and back into the coelenteron, by alternating contraction and relaxation of the column muscles.

Even more pronounced than the decrease in $\dot{n}_{O_2}$ during aerial exposure is the

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of 25 μEinsteins $\cdot$ m^{-2} $\cdot$ s^{-1}. See text of Materials and Methods for explanation of treatment groups and expansion state (the latter ranging from 0: fully contracted to 4: fully expanded). Arrows indicate data during the hours of peak irradiance (689 and 696 μEinsteins $\cdot$ m^{-2} $\cdot$ s^{-1}), which were analyzed statistically. Analysis of variance indicated significant heterogeneity among the mean expansion states (F = 70.998, df = 6, $P < .001$). Treatment groups having means not significantly different (Student-Newman-Keuls multiple comparison test) at $P = .001$ share superscripts.

decline in net oxygen production by the zooxanthellae (P_z net) (Fig. 2; Table I). This is doubtless due to the shading of the algae when the anemone retracts its tentacles and contracts its marginal sphincter, covering its oral disk. Desiccation reduces the rate of photosynthesis in intertidal macroalgae (Brinkhuis *et al.*, 1976; Beer and Eshel, 1983), but this is not a factor in the present study, as anemones were exposed to humid air in closed respirometers, and the tissue water content upon their removal from the respirometers was the same as in unexposed anemones (77%). The large variation in oxygen fluxes in anemones during daylight (Fig. 2) probably arises from individual behavioral differences, specifically, the extent to which the oral disk is covered and thus the degree of shading of the zooxanthellae.

Although *A. elegantissima* is as productive as sympatric macroalgae (Fitt *et al.*, 1982), this conclusion is based on short-term measurements of photosynthesis in submerged specimens. Because of the large decrease in P_z net due to shading during contraction in air, productivity estimates for this intertidal sea anemone must be reduced to the extent that populations are exposed to air during the tidal cycle. Such is not the case in many high intertidal macroalgae, which do not reduce photosynthesis during emersion (Johnson *et al.*, 1974; Quadir *et al.*, 1979; Beer and Eshel, 1983).

Because contraction to reduce desiccation during aerial exposure decreases zooxanthella photosynthesis more than it does animal respiration, the contribution of the zooxanthellae to the intertidal animals' respiratory carbon requirement (CZAR) is also significantly reduced when compared with the subtidal anemones (Table I). When oxygen flux in high shore anemones was measured during continuous immersion (Fig. 2), there was no significant difference in P_z net between these specimens and true low shore anemones, yet CZAR in the high shore individuals was significantly greater (Table I). This was largely due to the lower respiration rate in the high shore anemones under subtidal conditions, which may represent their "conservationist" approach to energy utilization (Newell and Branch, 1980; Shick, 1981).

Our values of 34% for CZAR in low shore *A. elegantissima* and 42% in high shore conspecifics during continuous immersion are in good agreement with that of 45% obtained by Fitt *et al.* (1982). The actual value of CZAR depends, *inter alia*, on the percentage translocation of algal photosynthate to the animal host, and both of these studies used the conservative figure of 40% based on Trench's (1971) ^{14}C-translocation experiments. These calculations of CZAR also depend on the rate of respiration by the zooxanthellae, which is not measured but rather assumed to be in direct proportion to their biomass fraction ($1-\beta$) of the entire symbiosis (Muscatine *et al.*, 1981). This assumption does not incorporate any possible scaling effects on mass-specific $\dot{n}_{O_2}$ in algal unicells and intact animal tissues, so algal respiration may be greater and P_z net lower than assumed. More recently, based on rates of carbon fixation, and zooxanthella biomass and doubling time, Muscatine *et al.* (in press) have suggested that translocation of photosynthate from algae to host may be greater than 40%, perhaps twice what was accepted previously. If true, this would double the value of CZAR and push *A. elegantissima* much closer to full photoautotrophy with respect to respiratory carbon than our results and those of Fitt *et al.* (1982) indicate. Regardless, these caveats do not alter our basic finding that intertidal exposure greatly reduces photosynthesis and hence CZAR in *A. elegantissima*, and must in turn place a premium on the efficiency of capture and utilization of prey in high shore individuals (Zamer and Shick, in prep.).

Surprisingly, net oxygen production by both low and high shore *A. elegantissima* reached its peak before maximum light intensity occurred, and oxygen production actually declined during the period of highest irradiance (Fig. 2). Observations of anemones in the respirometers indicated that the decline in photosynthesis coincided

with contraction, even by immersed anemones, in very bright light. Even in air the anemones were partly expanded (oral disk exposed and coelenteron being irrigated) under cloudy-bright conditions, but they contracted in full sunlight. The greatest variability in the oxygen flux data consistently was found just as photosynthesis was reaching its maximum and before the highest irradiance occurred (Fig. 2). This may have been due to individual differences in photosensitivity and the onset of contraction during increasing light intensity. The similar transient decline in photosynthesis measured *in situ* during the brightest part of the day in shallow reef corals (Porter, 1980) and in *Tridacna squamosa* (Mangum and Johansen, 1982) may likewise reflect behavioral shading of the zooxanthellae.

Our observations of behavior are consistent with those of Pearse (1974), who noted that symbiotic individuals of *A. elegantissima* in tidepools remained fully expanded on slightly overcast days but contracted in midday sunlight on clear days. Pearse also suggested that the decline in photosynthesis under intense light was due to effects of light on maximally exposed zooxanthellae. However, photoinhibition of zooxanthellae apparently does not occur even at irradiances well above those in this study (Muscatine, 1980; Fitt *et al.*, 1982), and the observed decrease likely stems from the anemones' contraction to avoid the deleterious direct and indirect effects of light on both the animal and algal tissue. Therefore we performed a quantitative study of behavior to further examine this phenomenon.

The behavior experiments clearly showed that contraction by symbiotic anemones at midday was due both to effects of UV radiation and to oxygen produced within the anemones' tissues by their zooxanthellae (Fig. 3), with the latter having the greater effect. Notice that the "UV-blocked" anemones began to contract when the irradiance reached 200–300 μEinsteins $\cdot$ m$^{-2} \cdot$ s^{-1} (Fig. 3), the same level at which net oxygen production by anemones shielded from UV in the glass respirometers began to decline (Fig. 2). Later, as irradiance decreased in late afternoon, the anemones began to re-expand, resulting in a plateau in oxygen flux.

Aposymbiotic anemones (which normally inhabit deeply shaded crevices among the boulders on the jetty) showed greater contraction in bright sunlight than did DCMU-treated symbiotic anemones (Fig. 3), despite the elimination of zooxanthella-produced O_2 as a proximal cause of contraction in both groups. Buchsbaum (1968) found that ectodermal pigments in *A. elegantissima* were produced under the influence of bright light, and the aposymbiotic anemones from shaded habitats in our present study indeed had lower concentrations of UV-B absorbing substances than did symbiotic anemones.

In addition to their demonstrated role as a barrier against desiccation (Hart and Crowe, 1977), the gravel, shell debris, and fragments of macroalgae that *A. elegantissima* attaches to the verrucae on its column may act as a sunscreen to protect exposed anemones from harmful effects of sunlight (Shick and Dykens, 1982). Our casual field observations suggested that partially shaded anemones attached less debris than did anemones experiencing longer exposure to direct sunlight, and that previously shaded anemones cleaned of all debris and placed in full sunlight expelled their zooxanthellae (Dykens and Shick, in prep.). Pearse (1974) also noted the expulsion of zooxanthellae by anemones from shaded habitats when abruptly transferred to bright sunlight.

The relatively low I_k value (the breakpoint in the photosynthesis *versus* irradiance curve, which indicates the onset of maximum photosynthesis) of 120 μEinsteins $\cdot$ m$^{-2} \cdot$ s^{-1} in *A. elegantissima* (Fitt *et al.*, 1982) suggests that this symbiosis is adapted to low light availability. This may be related both to the turbidity of the water in the anemone's inshore habitat, as well as to the shading of the algae by the

anemone's contraction to avoid desiccation during aerial exposure. Because total chlorophyll ($a + c_2$) shows a pronounced seasonal cycle, with higher concentrations occurring during the winter months (Dykens and Shick, in prep.), we suggest that photosynthetic capacity in *A. elegantissima* is optimized both by physiological characteristics of the zooxanthellae (low I_k) and by variations in chlorophyll concentration related to total irradiance, which is a function of daylength, microhabitat, and local weather conditions. Because it is probably energetically advantageous for the anemone to maintain the maximum capacity for photosynthesis on a long-term basis, chlorophyll concentrations may reflect average light conditions at a given season in a particular microhabitat. This in turn may subject the animal tissue to unduly high levels of O_2 and superoxide radicals (Dykens and Shick, 1982), photosensitized oxygenations, and other chlorophyll-mediated photodynamic effects (Clayton, 1977) on unusually bright days. Accordingly, adaptation to these short-term fluctuations in irradiance are behavioral, including gravel attachment (Shick and Dykens, 1982, Dykens and Shick, in prep.) and contraction, which modulate the amount of light reaching the algal symbionts.

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